Author's responses

RC1' comments

Reviewer comments – egusphere-2025-4395 – Evaluation of the Particulate Inorganic Carbon Export Efficiency in the Global Ocean

Overview:

The research article by Jordan Toullec, entitled "Evaluation of the Particulate Inorganic Carbon Export Efficiency in the Global Ocean", explores particulate inorganic carbon export in the global ocean and discusses the role of various planktonic groups, differences between oceanic regions, and correlation with net primary production of particulate organic carbon.

Overall, the manuscript is interesting as it combines available data collected in the field, using sediment traps, for example, and satellite imaging. The amount of work transpires from all the data compiled, which is presented in the "Results" section. The discussion also targets a variety of processes, making it relevant. The "Materials and Methods" and "Results" sections are somewhat rich in information but not overly long, which is good, and the results also report on a variety of data that are well compiled together.

However, the reviewer believes that major revisions are required on the writing itself. The manuscript would benefit significantly from a deep review of the text. In numerous instances, sentence formulations are not appropriate, and missing words or repetitions make the text unnecessarily complicated to read in some parts. Consistency and flow are lacking, especially in the introduction and discussion, where the reader quickly gets lost in the amount of information. Similarly, verbs are missing in some instances, and sentences are not properly formulated. Nevertheless, the reviewer believes that a careful re-reading and re-writing of the above-mentioned sections of the manuscript by the author would decrease these issues significantly. The reviewer will then consider assessing the second version of the manuscript once these comments have been implemented. The reviewer also acknowledges that the author may not be a native speaker, but believes that with care given to the grammar and once all point-by-point comments added below have been implemented, another round of review will lead to a quality paper suitable for publishing.

AC: I sincerely thank RC1 for the careful reading of our manuscript and for the constructive feedback regarding the clarity and quality of the writing (Also highlighted by RC2). I fully acknowledge the concerns raised about sentence structure, consistency, and overall flow, particularly in the Introduction and Discussion sections. In response, I have thoroughly revised the entire discussion with particular attention to clarity, coherence, and readability. I have carefully reformulated sentences where wording was inappropriate, corrected grammatical issues, removed repetitions, and ensured that all statements are complete and syntactically correct. I believe that these revisions have significantly improved the overall readability and scientific clarity of the manuscript.

I appreciate RC1 understanding and constructive guidance, and I hope that the revised version now meets the standards required for publication in Biogeosciences. Please find below my justification and responses to comments.

Comments:

Line 8: I believe this should read “calcifying” rather than “calcified” (same throughout the text).

AC: The term has been modified, throughout the text

Line 9: same as above.

AC: The term has been modified

Line 24: instead of “due to”, I would advise using “through”.

AC: The sentence has been modified

Line 25: same as first comment.

AC: The term has been modified

Line 26: word missing, it should read “referred to as”.
AC: The sentence has been modified

Line 24-27: sentence is a bit overloaded, it would benefit from a rewrite, likely in 2 distinct sentences.
AC: The sentence has been separated into 2 distinct sentences:

Line 26: “Phytoplankton, through photosynthesis, uptake CO_2 and produce particulate organic carbon (POC). On the other hand, calcifying phytoplankton (such as coccolithophores), produce both POC and inorganic carbon (particulate inorganic carbon, PIC). Calcification process, often referred to as calcium carbonate ($CaCO_3$) production, releases CO_2, this is the counter pump effect.

Line 30-31: statement of “to estimate a particle/sinking flux” made twice, consider deleting one.

AC: The sentence has been modified

Line 31: “To measure a particle flux, the sediment traps and Thorium-234 activity (234Th activity) are the most widespread techniques, both in terms of time and geography (Savoye et al., 2006, Le Moigne et al., 2014).”

Line 40: I would slightly edit this sentence, as technically speaking, the calcification process removes alkalinity and releases CO_2. Later, once $CaCO_3$ has dissolved, I agree that alkalinity increases, as well as the uptake of CO_2. However, given that it is a “loop”, I think stating that it increases alkalinity and CO_2 uptake may be misleading. This would be up to the author to edit, but it should be considered.

AC: I agree with RC1 comment; to consider a “net” uptake of CO_2 from the atmosphere thanks to this process, the depth of dissolution should be implemented in the statement. I have deleted this part of the sentence.

Line 41: this should read “associated with”.
AC: The sentence has been modified

Lines 45-47: this sentence has no verb.

AC: My apologies for this absence. The sentence has been modified and separated into 2 distinct sentences:
Line 49: “The transfer efficiency (Teff,) corresponds to the proportion of exported organic matter that reaches the deep ocean. Teff is lower at high latitudes and higher at low latitudes (Henson et al., 2012).”

Line 64: this should read either “with a complex food web” or “with complex food webs”.
AC: The sentence has been modified:

Line 70: “are associated with a complex food web”

Line 78-79: the sentence is confusing; consider rephrasing.
AC: The sentence has been rephrased and separated into 2 distinct sentences:

Line 83: “Blooms of coccolithophores (e.g., Gephyrocapsa (Emiliania) huxleyi) can produce highly reflective patches at the ocean surface and exhibit distinctive optical properties (Balch et al., 1996, 2005; Balch and Mitchell, 2023). These optical signatures *can be used to estimate particulate inorganic carbon (PIC) concentrations and production rates at the global scale (Hopkins & Balch, 2018; Hopkins et al., 2019).”*

Lines 84-85: the paper from Kwon et al., 2024 states that 20% more CO2 would be emitted to the atmosphere if CaCO3 dissolution in the upper ocean did not occur. This does not necessarily mean that 20% more CO2 is captured. The formulation used here is misleading.

AC: The sentence has been reformulated:

Line 92: “Kwon et al. (2024) showed that without $CaCO_3$ dissolution in the upper ocean, approximately 20 % more CO_2 would be released to the atmosphere.”

Line 86: while the research article from Renforth and Henderson, 2017, is an important piece of work for carbon sequestration research, the reviewer expresses some concerns as to why it is used here. Aren’t there more suitable references? Please justify the use here.

AC: I agree with RC1’s comment that the two cited articles (Renforth & Henderson, 2017; Planchat et al., 2023) are not directly related to the specific processes of calcifying plankton production and dissolution fluxes, but rather to the role of alkalinity in controlling oceanic CO_2 sequestration and balance. Although these references do not specifically focus on calcifying plankton, they were included to acknowledge relevant studies addressing the broader role of PIC dynamics and alkalinity balance in regulating air–sea carbon exchange.

Line 95: “In addition, processes such as PIC production, sinking flux, and dissolution are key components of the ocean alkalinity balance, which in turn regulates atmospheric carbon uptake in surface waters (Renforth and Henderson, 2017; Planchat et al., 2023).”

Line 105: this should read “such as that PIC…”.
AC: The sentence has been modified:

Line 114: there is one too many “to”, it should read “integrated to 100 m using…”.
AC: The sentence has been modified:

Line 122: the link provided did not work at the time of the review. Please review and make sure that the data are accessible.
AC: Indeed, the web site has changed and is now referred as Hermes Globcolour (https://hermes.acri.fr/). The link has been changed in the text.

Lines 125-128: I do not fully understand the use of semicolons here. Commas would be more appropriate, and there is no need for capitalised words after the colon and semicolons.
AC: Thank you for pointing out my mistake, I modified the semicolons and changed the capitalised words, after the commas.

Line 130: please review the citation. I believe Biogesociences has specific formats for referencing websites, such as the date of access and further details. Please review.

AC: The website referencing has been reviewed. The date of last access has been added to the referencing (..., last access: 2 February 2024)

Line 137: why consider the first 200m for foraminifers and pteropods, while only considering the first 100m for coccolithophores?

AC: This discrepancy primarily reflects a technical limitation in the comparison between datasets. The global distribution of calcifying zooplankton taxa (foraminifers and pteropods) reported by Knecht et al. (2023) provides PIC standing stock estimates integrated over the upper 200 m, whereas global coccolithophore PIC standing stock is typically computed over the upper 100 m (Eq. 3; Balch et al., 2018). However, this difference in integration depth is unlikely to substantially affect the interpretation of our results. Coccolithophore abundance generally decreases markedly below 100 m depth, often becoming negligible or absent; therefore, PIC standing stock integrated over 100 m versus 200 m is expected to differ only marginally. Moreover, our discussion of global PIC standing stocks across taxa focuses primarily on their monthly climatology and seasonal variability, rather than on a strict quantitative comparison.

Line 158: I do not understand where the value of 388 comes from. Please elaborate.
AC: The value corresponds to the sum of sediment traps used in the dataset independently of the number of flux observations (i.e. multiple flux observations with the same sediment trap), this value differs of the 262 sediment trap locations because Multiple sediment traps may have been deployed on the same mooring line.

My apologies, the sum is 391 not 388. The value has been modified; the sentence has been clarified.

Line 189: “deployment” should be plural
AC: The sentence has been corrected

Line 202: I believe “coverage” should be used instead of “covering”, but this might need to be double checked.

AC: To avoid any ambiguity, the sentence has been revised.

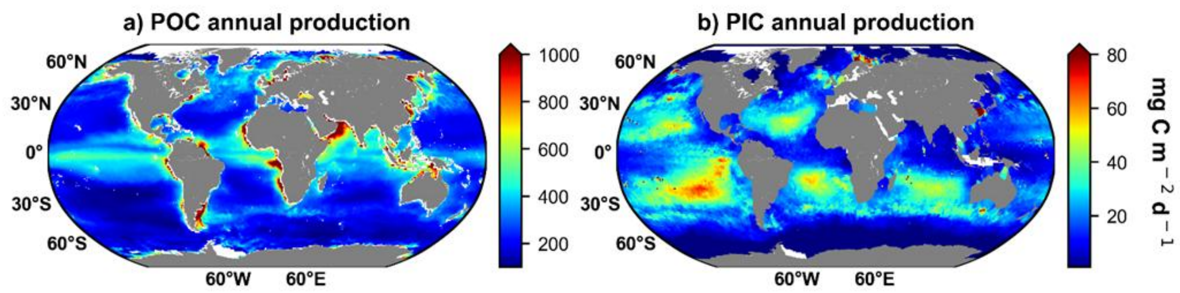
Line 224: “EZ PIC production values < 0.1 mg m $^{-2}$ d $^{-1}$ were removed from the dataset to exclude values close to zero or below the detection limit, which may result from a lack of satellite coverage.”

Line 204: “fecal pellet” should be plural.
AC: The grammatical agreement has been corrected, and this change has been applied to all other occurrences of the term “fecal pellet”.

Line 223: “regions” is missing.
AC: The words has been implemented

Line 224: in figure 2, could the tiles “a” and “b” be set on the same y-axis scale? The use of a logarithmic scale in “b” makes the direct comparison trickier. Please review whether it makes sense to put it on the same scale as “a” for easier comparison. If not, please provide the comparison in the response to reviewers.

AC: The logarithmic scale has been removed. Given that PIC production is much lower than POC production, the colorbars require different ranges to reflect the respective magnitudes (e.g., 100–1000 for POC and 1–80 for PIC production).



Line 253: this should read “gives us” and consider a full stop after “event” to separate the two trains of thought.
AC: The sentence has been rephrased:

Line 291: “This study highlights the importance of rapid calcification events. Satellite observations of coccolithophore blooms, which typically last less than 30 days, suggest that PIC fluxes from sediment traps should be integrated over short deployments rather than longer periods.”

Line 281: the sentence "NPP compared as compared to PIC" is misleading. Please edit accordingly.

AC: The sentence has been clarified

Line 320: "the correlation between PIC flux and NPP is generally higher than that between PIC flux and PIC production (Fig. 5)."

Line 285-287: the caption would benefit from some details as to what "n.s." means (which I believe is "no significant") and especially what value is considered "n.s."

AC: The caption has been implemented:

Line 326: "Non-significant correlations (p-value > 0.5, Pearson test) are indicated by "n.s."."

Lines 295-296: given that the 6 depths have already been discussed and introduced before, there is no need to add them here again (same as line 300). Only saying "at all depths" for the North Atlantic and "between 500 and 4000m in the North Indian Ocean" would lighten the text from numbers, making it more reader-friendly.
AC: The text has been modified accordingly

Line 368: "EZ PIC production and deep PIC flux are observed in the North Atlantic (100 to >4000m) and the Southern Ocean (100-500m and 1000-2000m). North Indian Ocean regions (subtropical areas) are also characterized by PIC production positively correlated with deep PIC flux (500 to 4000m, Fig. 6)."

Line 313-314: the start of the sentence is a bit awkward. Please revise.

AC: The sentence has been modified.
Line 354: "When mapped onto a 1° × 1° grid, the contributions of zooplankton fecal pellets and sinking phytoplankton aggregates exhibit a significant latitudinal pattern (Fig. 7 in Nowicki et al., 2022)."

Line 333: duplicate "in".
AC: The duplicate has been removed

Line 340: the formulation "and follow the pattern than zooplankton" does not make sense. Please revise.

AC: The sentence has been revised as:

Line 409: "and exhibits a pattern like that of zooplankton fecal pellet contributions to the gravitational pump (Fig. 7b)"

Line 356: "demonstrates" should not take an s here, and please review the sentence as it does not sound correct.

AC: The sentence has been revised

Line 336: "At the global scale, our results indicate that EZ PIC production is not correlated with PIC flux in the upper ocean."

Line 365: this should either read "there is a large uncertainty in the…" or "there are large uncertainties in the…".

AC: The sentence has been revised:

Line 386: "Total $CaCO_3$ production in the water column remains highly uncertain, with current estimates ranging from 0.7 to 4.7 Pg C yr^{-1} (Berelson et al., 2007; Buitenhuis et al., 2019; Lee, 2001)."

Lines 376, 377, 380: "coccolithophore" should be plural (check throughout the text)

AC: The plural has been checked throughout the text, when 'coccolithophore(s)" where used.

Line 385: "fecal pellet" should be plural (check throughout the text)

AC: The plural has been checked throughout the text, when 'fecal pellets" where used.

Line 392: the sentence is not correct. Please review.

AC: The entire paragraph has been revised:

Line 495: "In this study, the "packaging factor" theory is proposed as an important driver of the discrepancy between estimated PIC production and export flux across distinct oceanic regions. Despite the PIC/POC production ratio being twice as high in subtropical regions compared to temperate and subpolar regions, PIC export efficiency (PIC Eeff) is estimated to be tenfold lower and PIC transfer efficiency (PIC Teff) 1.5-fold lower. Our results suggest that zooplankton functional diversity and biogeography may explain the contrasting patterns of $CaCO_3$ export efficiency, through differences in dissolution and preservation within particles. Such processes could substantially contribute to total downward carbon export and associated nutrient fluxes. However, only a limited number of experimental studies have directly demonstrated the effect of zooplankton functional diversity on $CaCO_3$ dissolution. To test and refine the hypothesis proposed here, there is *a strong need for experimental data and in situ observations addressing both mesozooplankton and microzooplankton grazing dynamics and $CaCO_3$ fluxes.*

In the context of surface ocean warming and acidification, phytoplankton losses due to microzooplankton grazing in eutrophic waters are expected to increase (Chen et al., 2012), potentially attenuating the carbonate pump in temperate regions. In addition, POC export is unlikely to respond uniformly across high-latitude regions to future changes in ballast availability, which may also affect the biological carbon pump (BCP). Data compilations and model outputs indicate that coccolithophores tend to become less calcified relative to growth under increasing CO_2 concentrations (Krumhardt et al., 2017, 2019). End-of-century CO_2 projections suggest an approximately 11% decline in global oceanic calcification relative to preindustrial levels (Krumhardt et al., 2019). Such changes in surface ocean dynamics are expected to alter the future balance of surface alkalinity and CO_2 exchange between the ocean and atmosphere (Planchat et al., 2024; Tyrrell, 2008; Volk and Hoffert, 1985).”

Line 396: “layer” should be plural.
AC: Layers is plural now

Line 397: ”regardless of the respective depths of calcite and aragonite saturation” does not make sense. While I understand the idea, the sentence is not correct. Please edit.
AC: The entire paragraph has been revised (see my answer above):

“Once $CaCO_3$ is packaged into aggregates or fecal pellets, it is expected to be protected from surrounding seawater and associated dissolution processes. Consequently, $CaCO_3$ may avoid dissolution controlled by the saturation depths of calcite and aragonite.”

Line 400: change “in there” to “therein”.
AC: The entire paragraph has been revised (see my answer above)

line 420: here “suggest” should take an s.
AC: An s has been added to “suggest’

line 424: here it should read either “microzooplankton vacuoles induce PIC dissolution” or “microzooplankton vacuole induces PIC dissolution”.
AC: The sentence has been revised (‘microzooplankton vacuole induces PIC dissolution’)

Lines 429-431: the sentence is misleading, consider separating into 2 distinct sentences.

AC: The entire paragraph has been revised (see my answer above)
"However, ecosystem differences in microzooplankton grazing, particle export flux, and trophic structure have been largely underestimated. This limitation affects biogeochemical models that aim to predict the role of microbial communities in oceanic carbon flux."

Line 443-445: I am not fully sure I agree that blooming is an avoidance mechanism. Please argue your thoughts, but consider editing the sentence.

AC: I edited the sentence to precise my thoughts
Line 447: "G. huxleyi, can temporarily escape microzooplankton grazing during bloom onset through predation-avoidance traits, including colony formation, increased cell size, spines, or toxin production (Irigoien et al., 2005; Monteiro et al., 2016)."

Line 445-447: this sentence is not correct. It should read "could produce so much biomass that...", "won't" should be edited to "will not" ... Please review.
AC: The entire paragraph has been revised (see my answer above)

Line 448: the use of "regarding" does not make much sense here. Similarly, the sentence is confusing. Please edit.
AC: The entire paragraph has been revised (see my answer above)

Line 453: this should read "a mesocosm" study. Otherwise, "the mesocosm study from XXX".

AC: The sentence has been modified
Line 454: "a mesocosm study demonstrated..."

Line 455-456: why is "E. huxleyi" used here, while throughout the author used G. huxleyi? Please edit for consistency.
AC: My apologies for this confusion. The genus has been modified (*G. huxleyi*)

Line 461: the end of the sentence does not make sense. Consider changing "more" to "higher" or equivalent. Please edit.

AC: Higher has been implemented (instead of 'more')

Line 462: I am not sure how phytoplankton phenology is a time-dependent concept, why saying "During [...] phytoplankton bloom phenology"? Please edit.

AC: I agree with RC1, 'phenology' should not be included here. The entire paragraph has been revised (see my answer above)

Line 477: here, "that" should be added after "showed". Please edit.
AC: The term has been added after 'showed'

Line 489: duplicate of "In subtropical areas" from the previous sentence. Consider deleting.

The duplicate has been deleted

Line 507: please edit to maintain consistency in abbreviation, especially regarding PIC Eeff and PIC Teff.

AC: Abbreviations (PIC E_{eff} et PIC T_{eff}) have been standardized

Line 512: duplicate of "effect". Please edit.
AC: The sentence has been rephrased:

Line 520: this should read "result in". Please review.

AC: "Result in" have been implemented

AC: The discussion structure has been entirely revised, also considering RC2 comments/suggestions. The new version of the discussion is more concise; subsection has been merged to reduce redundancies as much as possible. The ideas follow a logical order, until the conclusion. The highlights of this study raised by the results are summarized in Fig. 8, which highlights the novelty of this study (the figure also has been simplified).

The discussion is now shorter, and the highlight of this study is now a significant part of the discussion. I must mention that I use specific concepts known so far in the field to explain my results and build this story. Variability of PIC flux efficiency and biological mediated $CaCO_3$ dissolution is still underestimated at present and is in desperate need of new proof-of-concept studies. This is why my study matters, given that our understanding of the subject is still incomplete.

1. Discussion

4.1. Mesopelagic PIC Flux and Ballast Effect Hypothesis

The ballast hypothesis originates from correlations between POC flux and mineral fluxes (opal and $CaCO_3$) in deep sediment traps (Klaas and Archer, 2002). However, $CaCO_3$ export flux in the upper ocean does not correlate with transfer efficiency (Henson et al., 2012), suggesting that $CaCO_3$ does not significantly protect POC from degradation at mesopelagic depths. Ecosystem structure, rather than mineral ballast, might be the primary control on the biological carbon pump. François et al. (2002) proposed the "packaging factor" theory, suggesting that highly $CaCO_3$-productive systems also contain organisms that produce sinking fecal pellets, which efficiently deliver organic carbon to deep waters (e.g., Nowicki et al., 2022). In subtropical and equatorial upwelling regions, export flux is not always associated with mineral ballast (Le Moigne et al., 2014), highlighting spatial variability in biomineral inclusion and supporting the role of ecosystem structure and phytoplankton phenology. On a global scale, our results demonstrate that EZ PIC production is not correlated with PIC flux in the upper ocean. However, in specific bioregions (RECCAP2), significant correlations exist between EZ PIC production and deep PIC flux (North Atlantic, Southern Ocean, and North Indian Ocean; Fig. 6; Table S4). These observations suggest that ecosystem structure and phenology are more important than the ballast effect in controlling PIC E_{eff} and PIC T_{eff}.

4.2. Taxa Contribution to Global PIC Stock and Production

Global $CaCO_3$ production estimates remain uncertain, ranging from 0.7 to 4.7 Pg C yr^{-1} (Berelson et al., 2007; Buitenhuis et al., 2019; Lee, 2001). Contributions from coccolithophores, foraminifers, and pteropods vary widely. Pteropods are estimated to contribute 0.87–4.2 Pg C yr^{-1}, representing 20–89% of global $CaCO_3$ production (Gangstø et al., 2008; Lebrato et al., 2010; Buitenhuis et al., 2019). Foraminifers contribute 0.036–0.14 Pg C yr^{-1}, corresponding to 2–4% of global $CaCO_3$ production (Schiebel, 2002; Lebrato et al., 2010; Buitenhuis et al., 2019). Coccolithophores are estimated to account for ~90% of $CaCO_3$ production (Ziveri et al., 2023; Kruijt et al., 2026). Deep sediment traps recover significant amounts of foraminifers and pteropods (Table 1; Fig. 3 in Neukermans et al., 2023), whereas coccolithophores dominate surface stocks and production. These observations remain poorly understood in terms of taxon-specific contributions and highlight the need for additional proof-of-concept and process-based studies to better quantify ecosystem-specific controls on PIC production and export. This study demonstrates that, at the global scale, coccolithophores dominate the PIC standing stock. Moreover, seasonal variability in coccolithophore production and biomass appears to play a central role in regulating PIC export efficiency (Fig. 7).

4.3. Influence of Ecosystem Structure on PIC Export

The fraction of exported phytoplankton production that is remineralized is mainly influenced by ecosystem structure, which is linked to the seasonal amplitude of NPP (Fig. 7a). Blooms of diatoms and coccolithophores (e.g., *G. huxleyi*), which are expected to induce intense particle sedimentation, occur mostly in regions with high annual mean NPP and large seasonal amplitudes (Fig. 7a). In contrast, nanoplankton and picoplankton dominate global production in oligotrophic areas (low latitudes) characterized by low seasonal NPP amplitude (Lima et al., 2014). The ballast effect hypothesis, driven by biomineral inclusion (calcite and biogenic silica), has long been considered a mechanism enhancing particle export efficiency (PE_{eff}). In this study, PIC export efficiency (PIC E_{eff}; the proportion of PIC production exported from the surface) is generally higher north of 40°N and south of 40°S (temperate and subpolar regions). PIC transfer efficiency (PIC T_{eff}; the proportion of exported PIC reaching the deep ocean) is higher between 40°N and 40°S (subtropical regions) and exhibits a pattern like that of zooplankton fecal pellet contributions to the gravitational pump (Fig. 7b). Considering the main particle types involved in the gravitational pump (Nowicki et al., 2022), phytoplankton aggregates may enhance PIC E_{eff}, whereas zooplankton fecal pellets may enhance PIC T_{eff}. The following sections explore the mechanisms underlying these patterns.

4.4. "Biological Gatekeeper" of the mesopelagic PIC Flux

4.4.1. Packaging Factor and Aggregate Contribution

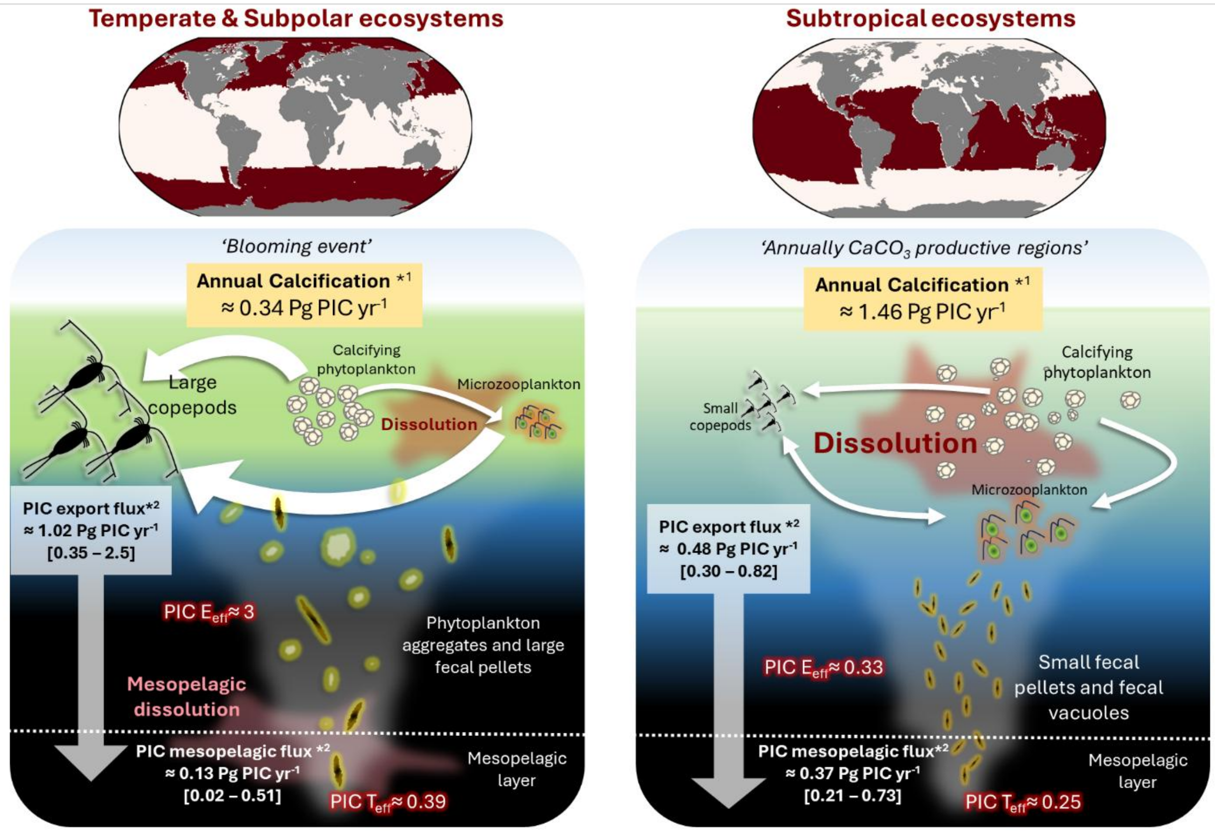
The packaging factor theory (François et al., 2002) suggests that subtropical and equatorial $CaCO_3$-rich ecosystems produce fast-sinking fecal pellets, thereby enhancing PIC export. In this study, the particle-dependent export model (Nowicki et al., 2022; Fig. 7b) shows that fecal pellet contributions are higher in these $CaCO_3$-rich ecosystems (subtropical and equatorial regions). However, observed PIC fluxes are lower in subtropical and equatorial regions despite higher production, challenging the hypothesis that $CaCO_3$ packaged in fecal pellets is protected from dissolution. Opal-dominated systems (temperate and subpolar regions) exhibit high PIC fluxes, suggesting that labile aggregates may also enhance PIC transfer and export efficiency (PIC E_{eff}). Overall, PIC production in the euphotic layer appears to be decoupled from PIC export and transfer efficiencies (PIC E_{eff} and PIC T_{eff}). Upper-ocean PIC loss is primarily attributed to biologically mediated dissolution (Morse et al., 2006; Friis et al., 2006; Buitenhuis et al., 2019; Sulpis et al., 2021; Dean et al., 2024). Although zooplankton and bacterial activity decrease with depth (Hernández-León et al., 2020), epipelagic and mesopelagic grazing still appears to contribute to PIC loss.

4.4.2. Hypothetical Processes of Biological-Mediated PIC Dissolution

Heterotrophic bacteria colonizing $CaCO_3$ particles appear to induce minimal dissolution, suggesting a limited role in PIC loss during sinking (Bissett et al., 2011). Similarly, the increase in hydrostatic pressure experienced by *G. huxleyi* aggregates during sedimentation does not significantly enhance calcite dissolution (Tamburini et al., 2021). Experimental and modeling studies also show that calcite is largely preserved during zooplankton gut passage, with dissolution generally low or negligible across various species and conditions (Harris, 1994; Honjo, 1976; Roth et al., 1975; Langer et al., 2007; Jansen and Wolf-Gladrow, 2001; Antia et al., 2008; Toullec et al., 2022; Dean et al., 2024). Despite lower contributions of fecal pellets to the gravitational pump at high latitudes (Fig. 7b), PIC export efficiency (PIC E_{eff}) remains elevated in these regions (temperate and subpolar areas), suggesting that additional factors, likely related to plankton community composition and phenology, play an important role in controlling PIC preservation and export.

4.5. Ecosystem control on PIC flux

Microzooplankton (<200 μm) play a central role in regulating primary producer biomass and facilitating carbon export via fecal vacuoles or aggregates (McNair et al., 2021; Calbet and Landry, 2004). Their grazing intensity exhibits strong latitudinal variation, ranging from 59% of annual primary production in temperate-polar regions to 75% in tropical-subtropical regions (Calbet and Landry, 2004). These patterns align with the observed latitudinal distribution of PIC export efficiency (PIC E_{eff}) and PIC transfer efficiency (PIC T_{eff}) (Fig. 7). In the North Atlantic, microzooplankton consume 288–589 mg C m^{-2} day^{-1} in the mixed layer during mid-summer, representing 39–115% of local phytoplankton production (Burkill et al., 1993), highlighting their substantial contribution to particle processing and carbon flux. Blooming coccolithophores, such as *G. huxleyi*, can temporarily escape microzooplankton grazing during bloom onset through predation-avoidance traits, including colony formation, increased cell size, spines, or toxin production (Irigoien et al., 2005; Monteiro et al., 2016). Conversely, subtropical and equatorial regions, characterized by low seasonal variability in coccolithophore biomass and continuous grazing pressure, experience sustained PIC loss, possibly due to dissolution within microzooplankton vacuoles (Antia et al., 2008; Dean et al., 2024). Large zooplankton may indirectly enhance PIC preservation by suppressing microzooplankton biomass and repackaging coccoliths into fast-sinking fecal pellets (Nejstgaard et al., 1994). Indeed, a mesocosm study demonstrated that ingestion rates of the large copepod *Calanus finmarchicus* were similar during blooms of diatoms and *G. huxleyi* (Nejstgaard et al., 1994). However, *C. finmarchicus* biomass increased threefold more in mesocosms dominated by *G. huxleyi* compared to those dominated by diatoms at similar algal biomass (Nejstgaard et al., 1994). The authors suggested that, during bloom conditions, copepods preferentially graze on microzooplankton. The incorporation of coccoliths into large fecal pellets (produced by mesozooplankton) likely results from passive, non-selective feeding behavior (e.g., current feeding), rather than from selective grazing on coccolithophores. Our dataset reveals a positive correlation between PIC production and PIC flux in the North Atlantic across all depth layers (Fig. 6), emphasizing the role of zooplankton-mediated carbon transfer (Hernández-León et al., 2020). Zooplankton functional traits vary among bioregions (Benedetti et al., 2023): temperate and subpolar regions are dominated by large, detritivorous or omnivorous copepods that feed passively (current- or cruise-feeders; Fig. 5 in Benedetti et al., 2023), whereas subtropical and equatorial regions are dominated by smaller, carnivorous copepods that feed actively (ambush- or current-ambush-feeders). Grazing by these distinct functional groups shapes phytoplankton biomass and community structure, ultimately influencing the efficiency and depth of PIC export (Le Quéré et al., 2016; Vallina et al., 2014; Fig. 8). The present study suggests that, in temperate and subpolar ecosystems, large copepods may enhance PIC export efficiency in two ways: (1) by repackaging coccoliths into fecal pellets through passive current feeding; and (2) by exerting strong grazing pressure on microzooplankton, thereby indirectly reducing $CaCO_3$-mediated dissolution within microzooplankton vacuoles (Dean et al., 2024; Fig. 8). In contrast, marine snow aggregates may create microenvironments that promote PIC dissolution in the mesopelagic layer, potentially explaining the observed decrease from PIC E_{eff} to PIC T_{eff} in temperate ecosystems (Fig. 8). Subtropical regions, on the other hand, exhibit continuous grazing, efficient nutrient recycling, and more complex food webs. Microzooplankton strongly regulate primary producer biomass and particulate organic carbon transfer, a fraction of which may subsequently be exported as fecal pellets or aggregates (McNair et al., 2021). This ecological context may favor $CaCO_3$-mediated dissolution within microzooplankton vacuoles (Fig. 8), potentially reducing PIC export efficiency (PIC E_{eff}).



*1 Satellite based NPP, excluding continental margin (200m depth) and interior sea

*2 Estimates based on the sediment trap annual PIC flux (g C m^{-2} yr^{-1}) extended to the total surface area. Results are expressed by the median and interquartile [q25 – q75]

Figure 8: Synthesis of the potential PIC pathway through the water column, in two distinct ecosystems: a) Subtropical ecosystems (subtropical gyres and equatorial upwellings). b) Temperate zone (North Atlantic, North Pacific and subpolar regions). The white arrows represent the trophic transfer between the different planktonic compartments (Predator prey), and double arrow means that both compartments

could be both prey and predator each other. Small copepods correspond to individual body sizes ranging from 200 µm to 2 mm; Microzooplankton (mostly protists, < 200 µm) represent the flagellates and ciliates community; Large copepods correspond to individual body sizes larger than 2 mm (mostly large calanoid). Note that microzooplankton could be heterotrophic, autotrophic or mixotrophic.

This study integrates the main conceptual frameworks currently proposed in the field to interpret the observed patterns in PIC export efficiency (PIC E_{eff}) and biologically mediated $CaCO_3$ dissolution. Our results highlight that variability in PIC E_{eff} and the mechanisms regulating $CaCO_3$ dissolution remain insufficiently constrained, particularly across contrasting biogeographical regimes. These findings underscore the need for targeted proof-of-concept and process-based studies to better quantify ecosystem-specific controls on PIC export. Improving this mechanistic understanding is essential for refining predictions of the oceanic carbon cycle under ongoing environmental changes.

RC2' comments

The manuscript by Toullec provides a comprehensive analysis supported by global ocean sediment traps data, ocean color satellite measurements and models to understand PIC fluxes, its export and transfer efficiency in the global ocean, and the role of plankton phenology in determining the PIC fluxes and standing stock. The analysis is strong and well structured and demonstrates a high level of knowledge also supported by relevant literature in the field.

I found the study an important and timely contribution in the understanding of global ocean carbon fluxes, the biological carbon pump and the carbonate pump, under fast-changing global ocean scenarios due to anthropogenic CO2 rise. The study is also very relevant in ocean-atmosphere interactions processes and CO2 balance.

While highlighting important processes in a very complete and comprehensive way, with appropriate methodology and statistical tools, I found the overall manuscript hard to read , encountering difficulties in following the argumentations for the way the manuscript is structured, for the long sentences, at times truncated (verbs missing), and for the variety of concepts and arguments introduced several times at different points. Therefore I suggest a thorough revision of the language and of the sections for clarity and smoothness of the text and a re-organization of the discussion sections with less sub-headings and with more highlights on novel concepts and differences to what has been known so far in the field (that I found hard to identify in the overall text). In particular, I suggest organizing the introduction and discussion section with clear parts on how the present study addresses the discrepancies in the field and how it advances the knowledge or proposes new pathways and hypotheses. I honestly find it difficult to follow PIC/POC standing stock, Teff, PEeff argumentations and the taxa or processes responsible behind these estimates as these concepts are introduced several times but rather in an unstructured way. I suggest major revisions for this reason, but the underlying concepts in my opinion are there.

AC: I thank RC2 for the constructive feedback. I have thoroughly revised the manuscript to improve readability and clarity. Long sentences were simplified, missing verbs corrected, and the overall flow enhanced. The Introduction and Discussion have been reorganized to clearly highlight how the study addresses knowledge gaps and to emphasize novel findings. Key concepts are now presented in a coherent and structured manner, reducing repetition and improving the logical progression of the argument. I believe these changes significantly improve clarity while preserving the scientific rigor of the work. These aspects are also highlighted by RC1.

I appreciate RC2 understanding and constructive guidance, and I hope that the revised version now meets the standards required for publication in Biogeosciences. Please find below my justification and responses to comments.

Specific comments (with line numbers):

45-48: incomplete sentence

AC: The sentence has been clarified separated into 2 sentences

Line 49: "The transfer efficiency (Teff,) corresponds to the proportion of exported organic matter that reaches the deep ocean. Teff, is lower at high latitudes and higher at low latitudes (Henson et al., 2012)."

48-57: unclear text. I suggest revisiting. Why the BCP is boosted?

AC: Ballast hypothesis postulates that biominerals (e.g. calcite, biogenic silica) may increase aggregates sinking velocity (excess of density) thus increasing the BCP.

This paragraph has been revised (implemented and nuanced), with clearer structure:

Line 52: "Satellite-based estimates of net primary production (NPP) at low latitudes carry substantial uncertainties, potentially biasing PE_{eff} calculations (Henson et al., 2019; Ryan-Keogh et al., 2023; Weber et al., 2016). Recent AI-based models improve the link between deep-ocean particle flux measurements and satellite observations (Picard et al., 2024, 2025). While T_{eff} is not consistently correlated with $CaCO_3$ export flux (Henson et al., 2012), sediment trap data show that coccoliths and coccospheres are more efficiently transported when incorporated into fecal pellets or marine snow (Honjo, 1976; Pilskaln and Honjo, 1987; Guerreiro et al., 2021; Liu et al., 2022; Toullec et al., 2022). The "ballast effect," postulates that biominerals like $CaCO_3$ and biogenic silica are expected to increase particle density and sinking velocity (Iversen and Ploug, 2010; Laurenceau-Cornec et al., 2020). Hence, BCP is expected to be enhanced by biomineralizing plankton (coccolithophores, diatoms). Nonetheless, the ballast effect remains debated because upper-ocean $CaCO_3$ export flux is not always linked to particle transfer efficiency, leaving the ballast hypothesis controversial (Henson et al., 2012)."

58-60: greater lability of organic matter is associated with higher degradation rates, therefore I expect that this labile fraction is not exported to the deep ocean.

AC: I agree with RC2, greater lability and greater degradation rates should be associated with smaller export efficiency. To remove any confusion, the text has been modified accordingly:

Line 63: "Seasonal influence is an important factor affecting Teff of carbon to the deep sea. During phytoplankton blooms, the exported organic matter is more labile, which likely expect to reduce its transfer efficiency."

62: Are there more recent studies with respect to Lima et al 2014? I would expect a lower Teff for higher turnover at low latitudes for a variety of other biological processes also temperature mediated. Are there more in-situ observations? Or do you imply that in CaCO3 productive regions despite a fast turnover and high lability or organic matter, this organic matter is fast removed by the ballast effect?

AC: I suggested that in annually $CaCO_3$-productive regions (low latitudes), despite the rapid turnover and high lability of organic matter (associated with higher temperatures and an active microbial loop), organic matter may be transported thanks to the ballast effect.

Line 64: "In low latitudes, which are annually $CaCO_3$ -productive regions, some modelling and observational syntheses have demonstrated that PE_{eff} tends to be lower while T_{eff} is relatively higher (Henson et al., 2012; Lima et al., 2014)."

AC: In the next paragraph, I suggested that in annually $CaCO_3$ productive regions (lower latitude), the ballast effect could attenuate the apparent high turnover rate and high particles lability due to faster sinking rate (as a result, the particles would settle more quickly and have less time to be dissolved and remineralized) and so increase T_{eff}.

Line 69: "The 'packaging factor' theory suggests that CaCO3-dominated ecosystems (subtropics and equatorial area) are associated with a complex food web, and CaCO3 would be more tightly packaged in fast-sinking fecal pellets, associated with potential ballast effect on the POC (Laurenceau-Cornec et al., 2020)"

AC: Hence, the associated organic matter should be more rapidly removed by the ballast effect.

AC: A more recent study (Henson et al., 2019), suggests that the whole ecosystem structure, rather than just the latitude, is important in setting export efficiency. Huang & Fassbender (2024) observed latitudinal variation in PE_{eff} based on BGC-Argo float observations in the Southern Ocean, supporting the concept of latitudinal influence.

Henson, S., Le Moigne, F., & Giering, S. (2019). Drivers of carbon export efficiency in the global ocean. Global biogeochemical cycles, 33(7), 891-903.

Huang, Y., & Fassbender, A. J. (2024). Biological production of distinct carbon pools drives particle export efficiency in the Southern Ocean. *Geophysical Research Letters*, *51*(12), e2023GL107511.

AC: These more recent studies can be implemented in the revised manuscript:

Line 65: "In low latitudes, which are annually $CaCO_3$ -productive regions, some modelling and observational syntheses have demonstrated that PE_{eff} tends to be lower while T_{eff} is relatively higher (Henson et al., 2012; Lima et al., 2014, Huang & Fassbender, 2024). However, the most recent studies agree that the structure of the ecosystem is a major driver of PE_{eff} and T_{eff}, even more so than latitude (Henson et al., 2019)."

72: PCB = BCP?

AC: My apologies, the acronym has been changed

90: the depth of reference? I think 100-200 m (as in the methods section?) but I would clarify it here too.

AC: I indicated the depth (Euphotic zone, which depends of PAR & Kd_{490nm}).

Line 98: "This work examines the variability of euphotic zone PIC production and deep PIC flux"

95: how deep do ocean color sensors go?

AC: In general, most of the satellite ocean color signal (Modis, SeaWifs...) comes from the upper surface to 20–40 m of the ocean (Up to ~80–100 m in extremely clear oligotrophic waters). Not even 10m for very turbid waters. I added text about it:

Line 132: "Satellite ocean color observations are representative the near-surface optical properties (upper 20–40 m in open ocean conditions)."

Eq. 1: can acidification and rising temperature effects be included in the growth rate calculation for coccolitophores?

AC: The effect of temperature is already incorporated into the model formulation. Specifically, growth rates of *Gephyrocapsa huxleyi* increase with temperature up to an optimal maximum, as described in A New Approach to Estimating Coccolithophore Calcification Rates From Space (Hopkins and Balch, 2018). https://onlinelibrary.wiley.com/doi/abs/10.1002/2017JG004235

Regarding ocean acidification (OA), I agree that this is an important consideration. However, OA is not explicitly included in the model used in the present study, as this was beyond its intended scope. However, several modeling studies have incorporated OA effects explicitly. For example, Carbonate Chemistry and Coccolithophore Calcification in CMIP5 Models (Krumhardt et al., 2020, https://onlinelibrary.wiley.com/doi/abs/10.1029/2020GB006727) examined the response of coccolithophore calcification to increasing CO_2 concentrations. Their results indicate that most ocean regions exhibit reduced calcification as CO_2 increases and acidification intensifies. They project an approximately 11% decline in global oceanic calcification by the end of the century relative to preindustrial CO_2 levels. Notably, while coccolithophore abundance may increase in certain regions, cells tend to become more lightly calcified under elevated CO_2 conditions.

If the RC2's question is whether temperature and OA can, in principle, be used to model $CaCO_3$ production, then the answer is yes. Both factors are mechanistically linked to coccolithophore growth and calcification and have been incorporated into other modeling frameworks.

210: Can you specify the difference in estimation? How many months were used in the model?

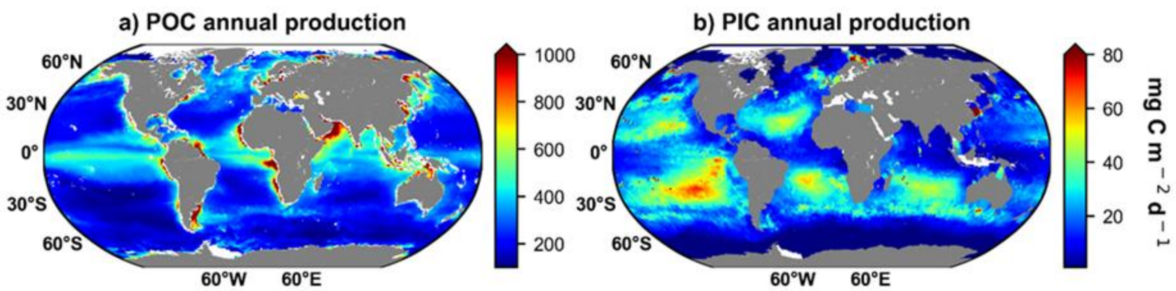
AC: I used 302 months into the model (sept 1997 to oct 2023), while Hopkins & Balch, 2018 integrated 144 months. Moreover, I used satellite merged products (AV-SWF, AVW-MERSWF, AVW-MERMODSWF, MODVIR, MODIS, see Table S1). Using the merged product, I expected broader ocean coverage: I implemented the sentence:

Line 232: "At the global scale, annual EZ PIC production of 1.65 ± 0.36 Pg C y-1 was estimated (monthly mean ± σ, 1997-2023 annual mean, 302 months of observation)"

Line 234: "The difference between the global estimates reported by Hopkins & Balch (2018) and those obtained in this study may be explained by the use of a merged satellite product (see table S1), which provides broader ocean coverage"

210-215: Can you add why NPP and PIC production are not concentrated in the same regions? Is it entirely due to plankton phenology?

AC: The discrepancy is mostly due to the favorable calcification conditions induced by the model (Temperature and EZ depth), there are characteristics of annually $CaCO_3$ productive regions.



NPP (POC production) is driven by nutrient availability (nitrate, phosphate, iron). Regions like upwelling zones or high-latitude oceans have high nutrient supply, so phytoplankton biomass and NPP are high (as you can see on the left Map). Whereases PIC production, especially by coccolithophores, is favored in nutrient-poor, stable waters (oligotrophic subtropical gyres), where coccolithophores can thrive and calcify efficiently.

The phenology also explains such patterns. In nutrient-rich regions, fast-growing diatoms dominate phytoplankton biomass and drive NPP, outcompeting coccolithophores (that can bloom later).

AC: I implemented the text:

Line 240: "NPP (POC production, Fig 2) is driven by nutrient availability (nitrate, phosphate, iron). Upwelling zones or high-latitude oceans have high nutrient supply, so phytoplankton production is high. Whereases PIC production, especially by G. huxleyi, is favored in nutrient-poor, stable waters (oligotrophic subtropical gyres), where coccolithophores can thrive and calcify efficiently"

220: Can you add why the difference in residence time between POC and PIC?

AC: Both PIC and POC residence time can result in a balance between dissolution/remineralization and sinking. To sink, both PIC and POC need to be aggregated (marine snow or fecal pellet). PIC can be attributed to abundance of free-floating coccoliths, that can be more accumulated at the surface than POC.

AC: POC can be readily consumed by bacteria, zooplankton, leading to rapid remineralization. PIC ($CaCO_3$) is chemically more resistant to biological degradation in the surface waters. It dissolves only under specific conditions (undersaturated carbonate waters, deep ocean or by biology).

AC: The text has been implemented:

Line 253: "Both PIC and POC residence times reflect a balance between sinking and removal processes such as dissolution or remineralization. For either to sink efficiently, aggregation into marine snow or incorporation into fecal pellets is generally required. PIC observation (ocean colors based) results mainly from free-floating coccoliths, which can accumulate at the surface to a greater extent than POC. In contrast, POC is readily consumed by bacteria and zooplankton, leading to rapid remineralization in the upper ocean. PIC ($CaCO_3$), however, is chemically more resistant to biological degradation in surface waters and typically dissolves only under specific conditions, such as in undersaturated carbonate waters, in the deep ocean."

250-255: unclear sentence/statement, suggest to revise.

AC: This paragraph has been reformulated:

Line 291: "This study highlights the importance of rapid calcification events. Satellite observations of coccolithophore blooms, which typically last less than 30 days, suggest *that PIC fluxes from sediment traps should be integrated over short deployments rather than longer periods"*

265-270: calcified taxa PIC stock does not correlate with PIC export flux on a global scale. This concept is repeated twice. However, here it is stated that coccolitophores dominate at high latitudes, previously it is stated that coccolitophores dominate the PIC standing stock, but it is also stated that PIC standing stock or production is higher at lower latitudes. So if not coccolitophores, who is dominating PIC standing stock at low latitudes?

AC: Coccolithophores always dominate the PIC standing stock (Fig. 3b). Coccolithophore can be co-dominant with pteropods at low latitude close to the equator (Fig. 4). In Fig. 4, any calcifying taxa standing stock demonstrates correlations with PIC export flux.

AC: The paragraph has been reformulated (the repetition has been deleted):

Line 305: The estimate of calcified taxa PIC stock, including coccolithophores, pteropods, and foraminifera, is not correlated with annual PIC export flux on a global scale (Fig. 4a). These estimates show that coccolithophores dominate the PIC standing stock, followed by pteropods and then foraminifera (Fig. 4). The latitudinal variation in PIC standing stock indicates an overlap between coccolithophore and pteropod PIC standing stock at the equator (Fig. 3b, 3e & Fig. 4b). *Coccolithophores and pteropods can contribute roughly equally to the PIC standing stock, but coccolithophores dominate at latitudes above 40°.*

279-283: unclear statement with some repetitions, can you rephrase?

AC: The paragraph has been reformulated:

Line 318: "No significant correlation is observed between log-transformed PIC flux and log-transformed NPP in the upper 100 m (Fig. 5). On average, although Pearson's correlation coefficients are low ($R^2 < 0.25$), the correlation between PIC flux and NPP is generally higher than that between PIC flux and PIC production (Fig. 5). At the deepest layer (>4000 m), however, the correlation between PIC flux and PIC production ($R^2 = 0.104$) exceeds that between PIC flux and NPP ($R^2 = 0.089$)."

Discussion Section: as already indicated, I strongly suggest to revise the structure of the whole section.

AC: The discussion structure has been entirely revised, also considering RC1 comments/suggestions. Please consider the new version of the discussion at the end of my responses to RC2 (below)

409-410: I find this sentence contrasting, to me very slight losses would agree with well-preserved coccoliths in fecal pellets.

AC: I agree with RC2 comment, this phrasing is confusing, I reformulated the sentence:

Line 432 "Experimental and modeling studies also show that calcite is largely preserved during zooplankton gut passage, with dissolution generally low or negligible across various species and conditions (Harris, 1994; Honjo, 1976; Roth et al., 1975; Langer et al., 2007; Jansen and Wolf-Gladrow, 2001; Antia et al., 2008; Toullec et al., 2022; Dean et al., 2024)."

Figure 8: what are the highlights and major findings of the present study, and its novelty? I think the results are not clearly evidenced as they are kind of hidden between different argumentations and references to previous works. I think it would be important to clearly describe Figure 8 that resumes the present study results and advancements in a sub-paragraph per-se.

AC: I agree with RC2. To highlight the novelty of this study, I have simplified Figure 8 and dedicated a specific paragraph to its discussion (4.4. Ecosystem control on PIC flux, see the updated text below).

The discussion structure has been entirely revised, also considering RC1 comments/suggestions. The new version of the discussion is more concise; subsection has been merged to reduce redundancies as much as possible. The ideas follow a logical order, until the conclusion. The highlights of this study raised by the results are summarized in Fig. 8, which highlights the novelty of this study (the figure also has been simplified). The discussion is now shorter, and the highlight of this study is now a significant part of the discussion. I must mention that I use every concept known so far in the field to explain my results and build this story. Variability of PIC flux efficiency and biological mediated $CaCO_3$ dissolution is still underestimated at present and is in desperate need of new proof-of-concept studies. This is why my study matters, given that our understanding of the subject is still incomplete.

2. Discussion

4.1. Mesopelagic PIC Flux and Ballast Effect Hypothesis

The ballast hypothesis originates from correlations between POC flux and mineral fluxes (opal and $CaCO_3$) in deep sediment traps (Klaas and Archer, 2002). However, $CaCO_3$ export flux in the upper ocean does not correlate with transfer efficiency (Henson et al., 2012), suggesting that $CaCO_3$ does not significantly protect POC from degradation at mesopelagic depths. Ecosystem structure, rather than mineral ballast, might be the primary control on the biological carbon pump. François et al. (2002) proposed the "packaging factor" theory, suggesting that highly $CaCO_3$-productive systems also contain organisms that produce sinking fecal pellets, which efficiently deliver organic carbon to deep waters (e.g., Nowicki et al., 2022). In subtropical and equatorial upwelling regions, export flux is not always associated with mineral ballast (Le Moigne et al., 2014), highlighting spatial variability in biomineral inclusion and supporting the role of ecosystem structure and phytoplankton phenology. On a global scale, our results demonstrate that EZ PIC production is not correlated with PIC flux in the upper ocean. However, in specific bioregions (RECCAP2), significant correlations exist between EZ PIC production and deep PIC flux (North Atlantic, Southern Ocean, and North Indian Ocean; Fig. 6; Table S4). These observations suggest that ecosystem structure and phenology are more important than the ballast effect in controlling PIC E_{eff} and PIC T_{eff}.

4.2. Taxa Contribution to Global PIC Stock and Production

Global $CaCO_3$ production estimates remain uncertain, ranging from 0.7 to 4.7 Pg C yr^{-1} (Berelson et al., 2007; Buitenhuis et al., 2019; Lee, 2001). Contributions from coccolithophores, foraminifers, and pteropods vary widely. Pteropods are estimated to contribute 0.87–4.2 Pg C yr^{-1}, representing 20–89% of global $CaCO_3$ production (Gangstø et al., 2008; Lebrato et al., 2010; Buitenhuis et al., 2019). Foraminifers contribute 0.036–0.14 Pg C yr^{-1}, corresponding to 2–4% of global $CaCO_3$ production (Schiebel, 2002; Lebrato et al., 2010; Buitenhuis et al., 2019). Coccolithophores are estimated to account for ~90% of $CaCO_3$ production (Ziveri et al., 2023; Kruijt et al., 2026). Deep sediment traps recover significant amounts of foraminifers and pteropods (Table 1; Fig. 3 in Neukermans et al., 2023), whereas coccolithophores dominate surface stocks and production. These observations remain poorly understood in terms of taxon-specific contributions and highlight the need for additional proof-of-concept and process-based studies to better quantify ecosystem-specific controls on PIC production and export. This study demonstrates that, at the global scale, coccolithophores dominate the PIC standing stock. Moreover, seasonal variability in coccolithophore production and biomass appears to play a central role in regulating PIC export efficiency (Fig. 7).

4.3. Influence of Ecosystem Structure on PIC Export

The fraction of exported phytoplankton production that is remineralized is mainly influenced by ecosystem structure, which is linked to the seasonal amplitude of NPP (Fig. 7a). Blooms of diatoms and coccolithophores (e.g., *G. huxleyi*), which are expected to induce intense particle sedimentation, occur mostly in regions with high annual mean NPP and large seasonal amplitudes (Fig. 7a). In contrast, nanoplankton and picoplankton dominate global production in oligotrophic areas (low latitudes) characterized by low seasonal NPP amplitude (Lima et al., 2014). The ballast effect hypothesis, driven by biomineral inclusion (calcite and biogenic silica), has long been considered a mechanism enhancing particle export efficiency (PE_{eff}). In this study, PIC export efficiency (PIC E_{eff}; the proportion of PIC production exported from the surface) is generally higher north of 40°N and south of 40°S (temperate and subpolar regions). PIC transfer efficiency (PIC T_{eff}; the proportion of exported PIC reaching the deep ocean) is higher between 40°N and 40°S (subtropical regions) and exhibits a pattern like that of zooplankton fecal pellet contributions to the gravitational pump (Fig. 7b). Considering the main particle types involved in the gravitational pump (Nowicki et al., 2022), phytoplankton aggregates may enhance PIC E_{eff}, whereas zooplankton fecal pellets may enhance PIC T_{eff}. The following sections explore the mechanisms underlying these patterns.

4.4. "Biological Gatekeeper" of the mesopelagic PIC Flux

4.4.1. Packaging Factor and Aggregate Contribution

The packaging factor theory (François et al., 2002) suggests that subtropical and equatorial $CaCO_3$-rich ecosystems produce fast-sinking fecal pellets, thereby enhancing PIC export. In this study, the particle-dependent export model (Nowicki et al., 2022; Fig. 7b) shows that fecal pellet contributions are higher in these $CaCO_3$-rich ecosystems (subtropical and equatorial regions). However, observed PIC fluxes are lower in subtropical and equatorial regions despite higher production, challenging the hypothesis that $CaCO_3$ packaged in fecal pellets is protected from dissolution. Opal-dominated systems (temperate and subpolar regions) exhibit high PIC fluxes, suggesting that labile aggregates may also enhance PIC transfer and export efficiency (PIC E_{eff}). Overall, PIC production in the euphotic layer appears to be decoupled from PIC export and transfer efficiencies (PIC E_{eff} and PIC T_{eff}). Upper-ocean PIC loss is primarily attributed to biologically mediated dissolution (Morse et al., 2006; Friis et al., 2006; Buitenhuis et al., 2019; Sulpis et al., 2021; Dean et al., 2024). Although zooplankton and bacterial activity decrease with depth (Hernández-León et al., 2020), epipelagic and mesopelagic grazing still appears to contribute to PIC loss.

4.4.2. Hypothetical Processes of Biological-Mediated PIC Dissolution

Heterotrophic bacteria colonizing $CaCO_3$ particles appear to induce minimal dissolution, suggesting a limited role in PIC loss during sinking (Bissett et al., 2011). Similarly, the increase in hydrostatic pressure experienced by *G. huxleyi* aggregates during sedimentation does not significantly enhance calcite dissolution (Tamburini et al., 2021). Experimental and modeling studies also show that calcite is largely preserved during zooplankton gut passage, with dissolution generally low or negligible across various species and conditions (Harris, 1994; Honjo, 1976; Roth et al., 1975; Langer et al., 2007; Jansen and Wolf-Gladrow, 2001; Antia et al., 2008; Toullec et al., 2022; Dean et al., 2024). Despite lower contributions of fecal pellets to the gravitational pump at high latitudes (Fig. 7b), PIC export efficiency (PIC E_{eff}) remains elevated in these regions (temperate and subpolar areas), suggesting that additional factors, likely related to plankton community composition and phenology, play an important role in controlling PIC preservation and export.

4.5. Ecosystem control on PIC flux

Microzooplankton (<200 μm) play a central role in regulating primary producer biomass and facilitating carbon export via fecal vacuoles or aggregates (McNair et al., 2021; Calbet and Landry, 2004). Their grazing intensity exhibits strong latitudinal variation, ranging from 59% of annual primary production in temperate-polar regions to 75% in tropical-subtropical regions (Calbet and Landry, 2004). These patterns align with the observed latitudinal distribution of PIC export efficiency (PIC E_{eff}) and PIC transfer efficiency (PIC T_{eff}) (Fig. 7). In the North Atlantic, microzooplankton consume 288–589 mg C m^{-2} day^{-1} in the mixed layer during mid-summer, representing 39–115% of local phytoplankton production (Burkill et al., 1993), highlighting their substantial contribution to particle processing and carbon flux. Blooming coccolithophores, such as *G. huxleyi*, can temporarily escape microzooplankton grazing during bloom onset through predation-avoidance traits, including colony formation, increased cell size, spines, or toxin production (Irigoien et al., 2005; Monteiro et al., 2016). Conversely, subtropical and equatorial regions, characterized by low seasonal variability in coccolithophore biomass and continuous grazing pressure, experience sustained PIC loss, possibly due to dissolution within microzooplankton vacuoles (Antia et al., 2008; Dean et al., 2024). Large zooplankton may indirectly enhance PIC preservation by suppressing microzooplankton biomass and repackaging coccoliths into fast-sinking fecal pellets (Nejstgaard et al., 1994). Indeed, a mesocosm study demonstrated that ingestion rates of the large copepod *Calanus finmarchicus* were similar during blooms of diatoms and *G. huxleyi* (Nejstgaard et al., 1994). However, *C. finmarchicus* biomass increased threefold more in mesocosms dominated by *G. huxleyi* compared to those dominated by diatoms at similar algal biomass (Nejstgaard et al., 1994). The authors suggested that, during bloom conditions, copepods preferentially graze on microzooplankton. The incorporation of coccoliths into large fecal pellets (produced by mesozooplankton) likely results from passive, non-selective feeding behavior (e.g., current feeding), rather than from selective grazing on coccolithophores. Our dataset reveals a positive correlation between PIC production and PIC flux in the North Atlantic across all depth layers (Fig. 6), emphasizing the role of zooplankton-mediated carbon transfer (Hernández-León et al., 2020). Zooplankton functional traits vary among bioregions (Benedetti et al., 2023): temperate and subpolar regions are dominated by large, detritivorous or omnivorous copepods that feed passively (current- or cruise-feeders; Fig. 5 in Benedetti et al., 2023), whereas subtropical and equatorial regions are dominated by smaller, carnivorous copepods that feed actively (ambush- or current-ambush-feeders). Grazing by these distinct functional groups shapes phytoplankton biomass and community structure, ultimately influencing the efficiency and depth of PIC export (Le Quéré et al., 2016; Vallina et al., 2014; Fig. 8). The present study suggests that, in temperate and subpolar ecosystems, large copepods may enhance PIC export efficiency in two ways: (1) by repackaging coccoliths into fecal pellets through passive current feeding; and (2) by exerting strong grazing pressure on microzooplankton, thereby indirectly reducing $CaCO_3$-mediated dissolution within microzooplankton vacuoles (Dean et al., 2024; Fig. 8). In contrast, marine snow aggregates may create microenvironments that promote PIC dissolution in the mesopelagic layer, potentially explaining the observed decrease from PIC E_{eff} to PIC T_{eff} in temperate ecosystems (Fig. 8). Subtropical regions, on the other hand, exhibit continuous grazing, efficient nutrient recycling, and more complex food webs. Microzooplankton strongly regulate primary producer biomass and particulate organic carbon transfer, a fraction of which may subsequently be exported as fecal pellets or aggregates (McNair et al., 2021). This ecological context may favor $CaCO_3$-mediated dissolution within microzooplankton vacuoles (Fig. 8), potentially reducing PIC export efficiency (PIC E_{eff}).

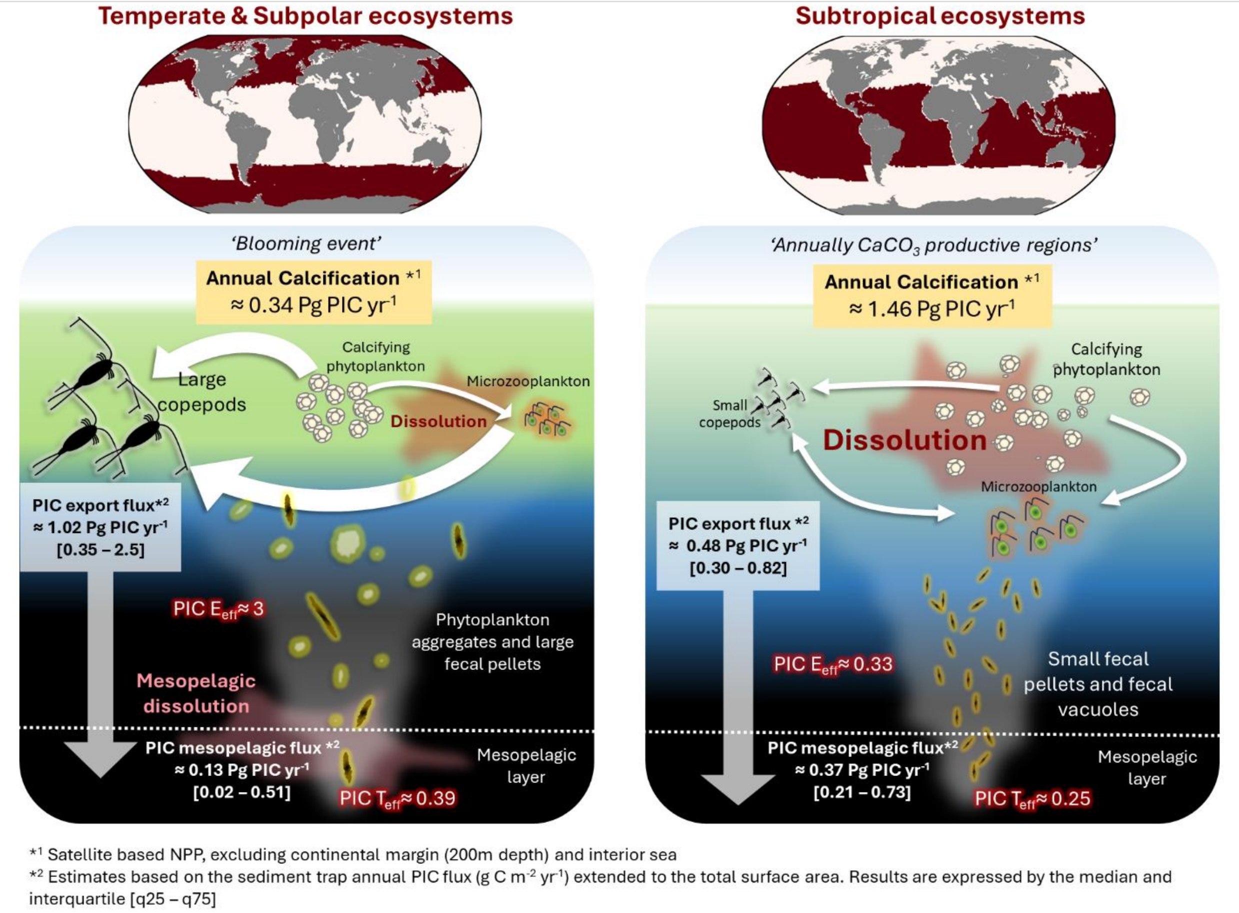


Figure 8: Synthesis of the potential PIC pathway through the water column, in two distinct ecosystems: a) Subtropical ecosystems (subtropical gyres and equatorial upwellings). b) Temperate zone (North Atlantic, North Pacific and subpolar regions). The white arrows represent the trophic transfer between the different planktonic compartments (Predator prey), and double arrow means that both compartments could be both prey and predator each other. Small copepods correspond to individual body sizes ranging from 200 µm to 2 mm; Microzooplankton (mostly protists, < 200 µm) represent the flagellates and ciliates community; Large copepods correspond to individual body sizes larger than 2 mm (mostly large calanoid). Note that microzooplankton could be heterotrophic, autotrophic or mixotrophic.

This study integrates the main conceptual frameworks currently proposed in the field to interpret the observed patterns in PIC export efficiency (PIC E_{eff}) and biologically mediated $CaCO_3$ dissolution. Our results highlight that variability in PIC E_{eff} and the mechanisms regulating $CaCO_3$ dissolution remain insufficiently constrained, particularly across contrasting biogeographical regimes. These findings underscore the need for targeted proof-of-concept and process-based studies to better quantify ecosystem-specific controls on PIC export. Improving this mechanistic understanding is essential for refining predictions of the oceanic carbon cycle under ongoing environmental changes.